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VOL. 29 No. 1

BULLETIN

OF THE

TORREY BOTANICAL CLUB

JANUARY 1902

Supplementary Notes on the Erysiphaceae

BY ERNEST S. SALMON, F.L.S.

Since the completion of my monograph (67)* on the Erysiphaceae, I have had the opportunity of examining a considerable amount of further material. This has enabled me to continue the study of the critical forms of several species; to investigate many cases of the reported occurrence of a species on an unusual host plant; and to extend the geographical range and add further hosts for many species. In the following pages will be found an enumeration of most of the species of the Erysiphaceae (following the order in which they are placed in my monograph) and under each species are arranged the critical notes, additional localities, host plants, etc. These records are based on personal examination, except in those cases in which they are followed by a number placed in brackets. These numbers indicate a published record, which will be found in the work of the author quoted under the respective number in the bibliography.

Before proceeding to give these notes, however, mention must first be made of several important papers dealing with the Erysiphaceae which have appeared recently. Of taxonomic interest, the following must be noticed. Hennings (31), in his "*Fungi japonici*," has described the following as new species or varieties: *Phyllactinia suffulta* var. *moricola*, *Microsphaera Japonica*, *M. sambucicola*, *Sphaerotheca Kusanoi*, *S. phtheirospermi*, *Uncinula Shiraiana*, *U. zelkowae*, *U. clandestina* forma *Japonica*, *U. verniciferae*,

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* Memoirs Torrey Club, Volume 9. The numbers refer to the bibliography which will appear at the close of the article.

[Issued 28 January]

and *Erysiphe pisi* var. *desmodii.* To this number of supposed new Japanese species, Sydow (82) has added another, viz. *Uncinula Kusanoi.* With one exception—*Uncinula verniciferae* P. Henn., which appears to be distinct—I consider that these Japanese plants are all to be referred to already described North American species, or to cosmopolitan ones. Notes on some of these Japanese plants will be found in my "Erysiphaceae of Japan" (68); the remaining species are discussed in the following pages.

The Erysiphaceae of South America have been noticed by Spegazzini (79) and also by Neger (52). The former author has described as a new species "*Erysiphe deserticola*" from the Argentine Republic, and has recorded other species of *Erysiphe* from the same country. The only specimens I have been able to see of "*E. deserticola*" have been in an immature condition, and I am inclined to think from these that the plant will prove to belong to the cosmopolitan species *E. polygoni* DC. The other South American species of *Erysiphe* recorded by Spegazzini prove to be *E. cichoracearum* DC. and *E. galeopsidis* DC. Of special interest is Spegazzini's (79, p. 330) record of the occurrence in the Argentine Republic and Uruguay of the conidial (*Oidium*) stage of members of the Erysiphaceae on no less than 98 different species of host plants—a fact which shows that these fungi flourish at all events in some parts of South America.

Neger (52) has described as new species, from the Argentine Republic, *Phyllactinia clavariaeformis, Microsphaera myoschili* and *Erysiphe Fricki. Phyllactinia clavariaeformis* proves to be identical with *P. antarctica* Speg., and although presenting somewhat remarkable characters which perhaps entitle it to be regarded as an incipient species—cannot be regarded as distinct from the old *P. corylea* (Pers.) Karst. The question of the relation of "*P. clavariaeformis*" to the type, is discussed in detail below, where mention is made of the fact that forms of *P. corylea* quite similar to the South American "*P. clavariaeformis*" appear sporadically on various hosts in Europe and Asia, along with all intermediate forms. *M. myoschili* is certainly only one of the forms of *M. alni* which show a much-branched apex of the appendages. *E. Fricki* is indistinguishable from *E. polygoni.*

In Europe Serbinov (76) has described from Russia a var.

borealis of *Microsphaera euonymi*, and a var. *polemoniacearum* of "*E. lamprocarpa* Lév." These two plants I have not seen, but the description given of the latter seems to show that it is a form intermediate between *E. cichoracearum* and *E. galeopsidis*.

In Japan a very distinct new species of *Uncinula*, *U. septata* Salm. (69) has appeared. The species has been found in two localities, and in each case it is associated with *Sphaerotheca lanestris* (*S. Kusanoi*).

From a geographical point of view, the record by Raciborski (60) of the occurrence of *Oidium*-forms in Java is noteworthy.

The occurrence of the New World species, *Sphaerotheca mors-uvae* (Schwein.)—the American gooseberry mildew—in a garden at Ballymena, County Antrim, Ireland, in 1900, is of special interest (see **71, 72**). The question of the possibility of its introduction from America is considered under the species.

Two important papers dealing with the Erysiphaceae by Grant Smith and Neger have appeared.

Grant Smith, in his paper, "The Haustoria of the Erysipheae," (**77**) has given a detailed account of the structure and development of these organs, and has added several interesting facts to our knowledge of the subject. While finding that the mature haustorium contains almost invariably a single normal nucleus (as Harper had already stated), the author records an isolated case, where the haustorium of "*Erysiphe communis*" on *Geranium maculatum* contained two nuclei. It was also found that occasionally haustoria have a septum in the neck portion. As has long been known, a mature haustorium is nearly always surrounded by a thick sheath-like layer. The correct interpretation of this sheath according to Grant Smith, is different from that which has hitherto been given. De Bary was of the opinion that it belonged to the protoplasm of the host cell, while Harper (Pringsh. Jahrb. wiss. Bot. **29**: 664), considered that this sheath is, as in the case of that of *Puccinia*, the disorganizing nucleus of the host cell. Smith says, however, that the sheath "does not belong to the protoplasm of the cell as de Bary supposed, nor is it the host nucleus as Rosen observed in *Puccinia*; but the contents of the sheath consist of disintegrated cellulose from the distal end of the cellulose ingrowth through which the haustorium has made its way. The bounding membrane of the sheath, on the other hand, is the plasmic membrane of the host cell stretched and greatly enlarged by the osmotic forces involved."

The haustoria of *Erysiphe graminis* are, as is well known, peculiar in being provided with long finger-like processes. These haustoria Smith has studied in detail, and shown well in several figures. With reference to these haustoria it is observed, "this form of absorbing organ may be looked upon as the result of a special effort of this species to obtain abundant food. The heavy growth of mycelium and the immense number of conidia produced by this species show the success it has attained. * * * Certainly these haustoria give an impression of activity not gained from other Erysipheae."

The most interesting discovery of Smith, however, is in connection with the haustoria of *Uncinula salicis.* Examples of *U. salicis* on *Salix discolor* were used for investigation, and the development of the haustoria was found to take place as follows: The mycelium (proper) is entirely external; on the upper surface of the leaf the lobed appressoria give rise to penetrating tubes which enter the epidermal cells. All of these tubes, however, do not (as in all other cases known) develop in the epidermal cells into haustoria. Although normal haustoria are formed abundantly in these epidermal cells, in addition numerous slender hyphae can be observed reaching from the outer walls across the epidermal cells to their inner walls. These hyphae are the penetrating tubes or necks of subepidermal but otherwise normal haustoria in the palisade cells. On the lower surface of the leaf, in a similar manner, some of the penetrating tubes reach into the mesophyll cells immediately under the epidermal layer, and form haustoria there.

Smith has also investigated the intercellular hyphae of *Phyllactinia*, and has found that occasionally the hyphae produce haustoria in the palisade cells. It was observed that the majority of the intercellular hyphae (which may consist of three to five, or perhaps more, or rarely of only two cells) take a more or less direct course towards the vascular bundles—a region abundantly supplied with available food; the fungus therefore shows a selective chemotropism.

Examples of *Phyllactinia* on *Xanthoxylum Americanum* were found to offer some striking differences with respect to the development of haustoria. The intercellular hyphae have thicker walls, and the intercellular appressoria are conspicuous, flattened, sucker-like structures pressed tightly against the cells of the leaf. So far as could be ascertained, these appressoria never give rise to the normal haustoria as in other examples of *Phyllactinia*, the only penetrating organs observed being minute tubes, bearing a vesicle apparently without protoplasmic contents. These latter Smith considers to be modified or stunted haustoria.

Neger's paper is entitled "Beiträge zur Biologie der Erysipheen" (52), and is a valuable contribution to our scanty knowledge of the subject. Some points in this paper I shall here criticise in detail, and at the same time record some observations I have made on the same subject.

Neger, by means of microtome radial sections, has carefully investigated the structure of the perithecial wall in many species of the Erysiphaceae. Summarized briefly, the following modifications of structure were found.

In *Erysiphe polygoni*, *E. cichoracearum* and *E. galeopsidis* no marked difference in the cellular structure of the lower and upper halves of the perithecium occurs. In *E. graminis*, and more markedly in *E. taurica*, the perithecial wall consists towards the exterior of several layers of very strongly thickened cells with an almost obliterated lumen. These layers of thick-walled cells are more numerous on the under than on the upper side. In consequence of this structure the perithecium becomes in a dry condition (on loss of turgescence) slightly concave on the upper surface, but never on the under surface. It may be noted here that Neger is incorrect in stating (on p. 365) that the genus *Erysiphe* (excluding *E. graminis*) is characterized by "Perithecien nicht dorsiventral," as in *E. taurica* and in many forms of *E. cichoracearum* (*e. g.* the large form on *Arctium*) the perithecium becomes in the dry state very strongly concavo-convex.

In the species of *Sphaerotheca* examined, no difference in the cellular structure of the wall in the lower and upper halves of the perithecium was found to exist; consequently the perithecium in drying contracts equally on all sides.

In the genus *Microsphaera* (*M. alni*, *M. euonymi*, *M. grossulariae*, *M. berberidis*, and *M. euphorbiae* were examined) a well-marked difference of structure in the perithecial wall distinguishes the upper from the lower side. The wall of the upper side of the perithecium is composed of thick-walled cells, and is consequently rigid, while the lower side, being composed of thinner-walled cells, is flexible. As the result of this structure the perithecium in drying becomes strongly concave on the lower surface—a fact, according to Neger's interpretation, of great biological importance.

Podosphaera resembles *Microsphaera* in the structure of the perithecia.

The genus *Uncinula* is divided by Neger into two groups—*Microsphaeroidea* and *Euuncinula*. In the first named group, in which the species *U. salicis*, *U. prunastri*, *U. macrospora*, *U. flexuosa*, *U. necator*, and *U. clandestina* were examined, the cellular structure of the perithecial wall resembles that found in the genus *Microsphaera*. In the species of this group *Microsphaeroidea*, however, the difference of structure between the tissues of the under and upper sides is even more marked. A rigid layer of cells with strongly thickened walls surrounds the perithecium on its upper surface and at the sides, while layers of delicate-walled cells having a wide lumen occur on the lower surface.

The group *Euuncinula* comprises *U. aceris*, *U. polychaeta*, and *U. circinata*. Here a differentiation exists between the cell-structure of the under and upper halves of the perithecium, but it is not identical with that found in the last group. In *U. aceris* the cells toward the upper surface have only slightly thicker walls and a slightly smaller lumen than those towards the lower surface; in *U. polychaeta* the same characteristics are more marked; in *U circinata*, however, exactly the converse is found. The perithecia of *U. aceris* (see monograph, p. 92) and of *U. polychaeta* become, when dry, concave on the under surface; while in *U. circinata*, in consequence of the tissue towards the upper surface being composed of tender cells with a wide lumen and those towards the under surface being relatively thick-walled, the perithecia never become concave on the under surface, but usually become slightly so on the upper.

In *Phyllactinia* the cells of the tissue towards the base of the perithecium have a narrower lumen than those towards the upper surface; consequently the perithecium in drying never becomes concave on the under surface.

Neger considers that the difference of structure in the upper and lower halves of the perithecium which is found in many species, and which in many cases causes the under surface of the perithecium to become strongly concave on loss of turgescence, is of great biological importance. In describing the ripe perithecium of *Microsphaera astragali*, he remarks (p. 351): "Die Fruchtkörper lösen sich, wenn sie einen gewissen Grad der Reife erreicht haben, vom Substrat los, indem sich die Unterseite der Perithecien bei abnehmendem Turgor einwärts wölbt und dadurch die Mycelfäden, an welchen das Perithecium entstand, zerrissen werden. Diese constant einseitige Einwärtswölbung kommt dadurch zu Stande, dass die Perithecienwand an der Oberseite einen starren, aus englumigen dickwandigen Zellen gebildeten Panzer darstellt, während die Zellen der Unterseite relativ weites Lumen und zartere Wände besitzen. * * * Es kann demnach kein Zweifel bestehen, dass wir es hier mit einer Einrichtung zu thun haben, welche eine spontane Loslösung der Perithecien vom Substrat ermöglicht. * * * Es sei gleich hier bemerkt, dass alle (von mir untersuchten) *Microsphaera-Podosphaera-* und die meisten *Uncinula*-Arten den gleichen Loslösungsmechanismus besitzen."

According to the behavior of the ripe perithecium, Neger divides the Erysiphaceae into the following biological groups:

A. Perithecia not spontaneously falling off, mostly attached to the mycelium by their appendages: *Sphaerotheca*, *Erysiphe* (*U. circinata ?*).

B. Perithecia falling off when ripe.

  1. Detachment caused by the shrinking of the perithecium base.

    (*a*) Cellular tissue of upper half of perithecium formed of narrow strongly thickened rigid cells; cells of lower half delicate-walled: *Podosphaera*, *Trichocladia*, *Microsphaera*, *Uncinula* (? *Microsphaeroidea*).

    (*β*) Cells of the perithecial wall of about the same size on the under and upper sides of the perithecium; on the upper side with narrow lumen, on the under with more or less delicate walls. Cells in the regions of the greatest curvature very large and flexible, becoming shrunken on the drying of the perithecium. The under surface of the perithecium consequently becomes concave. *Euuncinula* (excl. *U. circinata*).

  2. Detachment of the perithecium follows through the pressure exerted against the substratum by the appendages which turn downwards. The perithecium in drying suffers no important change of shape: *Phyllactinia*.

In connection with the statement made above that the detachment of the perithecium from the mother-mycelium is caused in many instances by the shrinking of the perithecium base, Neger remarks (p. 358): "Ich habe nun häufig beobachtet, dass die Reactionsfähigkeit der Perithecien auf Turgoränderungen sehr gross ist, d. h. dass bei Uebertragung eines Fruchtkörpers aus einem feuchtem Raum in einen Exsiccator die Gestaltveränderung sehr schnell erfolgt. Wäre es da nicht denkbar, dass bei der durch Turgorabnahme herbeigeführten Schrumpfung des Wandgewebes die Loslösung, d. h. Zerreissung der festhaltenden Mycelfäden, so gewaltsam erfolgt, dass das Perithecium eine starke Erschütterung erleidet und sich dabei auf die Seite legt (auch diese Lage ist an reife Perithecien sehr oft zu beobachten) oder sogar umkehrt? Es ist mir allerdings nicht gelungen, diesen Vorgang selbst zu constatiren."

Whether or not it be correct to consider that the detachment of the perithecium from the substratum is caused generally by the base of the perithecium shrinking and becoming concave, it may be noted that this contraction is, in one case at any rate, not essential to the process. This can be seen by observing ripe perithecia of *U. circinata*. Neger is in error in stating that the perithecia of this species do not spontaneously become free from the mycelium. If perfectly ripe examples of *U. circinata* are examined, *e. g.*, those in Ell. & Everh. Fung. Columb. n. 110 (in herb. Kew), it will be found that many of the perithecia are in a reversed position, *i. e.*, the apex of the perithecium, covered with the numerous appendages, is pressed against the surface of the leaf, while the base of the perithecium, to which there are usually a few mycelial threads attached, is exposed to view. The appendages of these fully ripe perithecia are always very numerous and well developed; and from Neger's remark that in the specimens examined by him the appendages were badly developed it is evident that he was dealing with immature material. The reversal of the perithecia of *U. circinata* mentioned above implies of course a spontaneous loosening of the perithecium from the mycelium. The perithecium, however, of this species does not, in consequence of its cellular structure (see above), become concave on the lower surface, so that it is evident that in the case of this *Uncinula* at all events some other cause brings about the detachment of the perithecium.

In many cases the perithecia of species of the Erysiphaceae appear to become free through the gradual dying away and disappearance of the mycelium.

Some observations I have made on the spontaneous detachment and reversal of the perithecium in some species of *Uncinula* may be mentioned here.

At p. 92 of my monograph I pointed out that the perithecia of *Uncinula aceris* are, from some cause, frequently turned over, and that the appendages which are thus pressed against the leaf, become mucilaginous and attach the (reversed) perithecium to the leaf. Some observations I have made since show that this phenomenon occurs in many other species of *Uncinula*. In *U. salicis* it can be seen on examining perfectly ripe examples that many of the perithecia have become turned over, so that the apices of the appendages rest against the surface of the leaf. This can be well seen in the specimens in De Thüm. Fung. austr. 655 (in herb. Kew). In a few instances, I have observed, in herbarium specimens, that the perithecia, through the mucilaginous degeneration of their appendages, have become actually fixed in this position to the leaf. It is easy to produce the same result artificially. A leaf after having been placed in water for a few minutes, and then freed from the superficial moisture, was laid on the surface of a leaf which bore numerous ripe perithecia of *U. salicis*—an example being chosen in which the appendages of the perithecia were spreading upwards. After a few hours, the superposed leaf was examined, and it was then found that several reversed perithecia were adhering by their appendages to its surface. These perithecia required a slight amount of force to be detached. Perithecia of *U. salicis* were placed upside down on damp leaves of *Hedera Helix*, and it was found after a short time that these had adhered to it by their appendages. In *U. macrospora*, *U. prunastri*, and *U. Clintonii* the same reattachment of the perithecia in a reversed position can be observed. An ivy-leaf, was laid upon a leaf of *Tilia Americana* bearing numerous perithecia of *U. Clintonii* in which the appendages were spreading upwards. After a few hours perithecia reversed and fixed by their appendages were found on the ivy-leaf.

On account of their large size, the reattachment of the perithecia can be most easily seen in *U. polychaeta.* In this species the very numerous crowded appendages spread widely, and attach the reversed perithecium by a film-like layer spreading beyond the diameter of the perithecium on every side. The mucilaginous breaking down of the walls of the appendages is very evident here, and the reattachment of the perithecium is as firm as that caused by the penicillate cells of *Phyllactinia.*

In *U. circinata,* also, if reversed perithecia are placed on a damp leaf, they will be found subsequently to have become attached to it by their appendages.

This phenomenon of the spontaneous freeing of the perithecium and its subsequent reattachment by the appendages has been the cause, I believe, of leading systematists into several curious errors. The first case that may be mentioned is that of "*Uncinula Columbiana* Selby," on *Scutellaria lateriflora* from the United States. This fungus, as I pointed out in my monograph, p. 86, agrees exactly in all its characters with *U. salicis.* *U. salicis* is only known to grow on species of *Salix* and *Populus,* and I suggested at the time that its presence on the *Scutellaria* was perhaps accidental. I feel now little doubt that we have here an instance in nature of the perithecia of *U. salicis* becoming attached by their appendages in the manner described above to a foreign substratum, in this case the leaves of a herbaceous plant. In a second case it seems quite certain that reversed perithecia of *U. salicis* attached by their appendages have been under observation. I refer to the "*U. salicis* var. *epilobii*" of Vestergren (Bot. Notiser, 1897: 256), which was described as growing at Upsala on *Epilobium angustifolium,* (see monograph, p. 87). In the description Vestergren remarks: "The most obvious presumption would be that the perithecia of the *Uncinula* in question had been transferred by the wind to the *Epilobium* from, *e.g.*, some *Salix* bushes growing in the neighborhood. Apart from the fact that there were none of the usual host-plants of *U. salicis* in the neighborhood, one must quite reject this presumption when one observes (under a slight microscopic magnification) how firmly the perithecia of the var. *epilobii* are fixed to the substratum by means of the appendages radiating on all sides." We may, I think, safely infer here that groups of perithecia of *U. salicis* must have been blown on the *Epilobium,* and adhered by the appendages in the manner described above.

In the case, also of Sredinski's (80) record of the occurrence of *U. salicis* on *Hedera Helix* the same explanation probably holds good.

I have seen also two specimens labelled "*Uncinula Wallrothii* on *Lonicera Xylosteum*." The perithecia of the *Uncinula* on this plant, I have ascertained, are in the majority of cases adhering, in a reversed position, by means of their appendages; and there is no reason for believing that the *Lonicera* was serving as a host-plant (see monograph, p. 97).

It will, in all probability, be found that the example of *U. geniculata*, occurring on leaves of *Hydrophyllum appendiculatum* (see monograph, p. 112) consists of perithecia attached by their appendages.

The following remarks of Neger's require criticism. Neger writes (54, p. 344): "Man hat bisher, wie aus den meisten *Erysipheen* behandelnden Werken (besonders soweit dieselben mit Abbildungen versehen sind zu entnehmen ist, allgemein an der ansicht festgehalten, dass die Perithecien aller Erysipheen annähernd gleichen anatomischen Bau aufweisen. Dies ist aber ein grosser Irrthum und es ist unverständlich, wie z. B. Tulasne in seiner Carpologia von *Sphaerotheca Castagnei* eine abbildung geben konnte, die, was Gestalt und relative Grösse der Perithecienwandzellen anlangt, durchaus nicht auf *Sphaerotheca*, sondern viel eher auf *Uncinula*, oder *Erysiphe* passt." Neger is apparently unaware that in *S. Castagnei* the size of the external cells of the perithecium varies from 10–40 μ wide. Under the old name "*S. Castagnei*" were included the two plants now known as *S. humuli*, in which the external cells of the perithecium measure from 10 to 20 μ wide, averaging 15 μ; and *S. humuli* var. *fuliginea*, in which the cells measure from 20–30, rarely 40 μ, averaging 25 μ wide (see monograph, pp. 45 and 49), Neger apparently intends by "*S. Castagnei*" the segregate last-named, since he remarks: "Die Wandzellen bei *Sphaerotheca* sind im Verhältniss zum Peritheciendurchmesser auffallend gross und sind von sehr unregelmässiger Gestalt, während die Wandzellen bei *Erysiphe*, *Uncinula* und anderen Erysipheen relativ viel kleiner sind und mehr oder weniger runde oder polygonale Gestalt besitzen. Z. B. für *Sphaerotheca* resp. *Uncinula* lässt sich das Verhältniss der Grösse einer

Wandzelle zum Peritheciendurchmesser durch folgende approximative Zahlen ausdrücken: 1:5 resp. 1 : 18." Now the size of the cells in the species of *Uncinula* varies from 10 to 15 μ wide, reaching rarely to 20 μ; so that it is perfectly correct to represent the perithecial wall of some forms of "*S. Castagnei*" as being of similar structure to that of species of *Uncinula*. As regards the proportion between the number of cells and the diameter of the perithecium also, *S. humuli* type agrees with species of *Uncinula*.

Neger, it may here be noted, has raised De Bary's section "*Trichocladia*" of *Erysiphe* to generic rank, and places in the genus *Microsphaera astragali* and *Erysiphe tortilis*. I consider this arrangement undesirable for the following reasons: The two genera *Microsphaera* and *Erysiphe* are undoubtedly very closely allied, and it seems to me to be more in accordance with the principles of a natural classification to include in these genera the species which on both sides approach each other, than to take these out and base a new genus on them. Further, if we follow Neger and place *M. astragali* in the new genus *Trichocladia*, it is clearly unnatural for *M. Bäumleri*, so closely allied, to be generically separated, and we should find it impossible to draw a satisfactory line between "*Trichocladia*" (including *M. Bäumleri*) and *Microsphaera*. It still seems to me to be better to include *M. astragali*, which although certainly approaching some forms of *E. polygoni*, yet on the other hand is closely allied to *Microsphaera Bäumleri* and *M. euonymi*, in the genus *Microsphaera*, and to keep *E. tortilis* in *Erysiphe* on account of its relationship with certain forms of *E. polygoni*.

Neger (**52**, p. 337) referring to the fact that I included in my monograph under the name *Erysiphe polygoni* all plants which showed certain morphological characters, notwithstanding that they grew on the most diverse host-plants—no fewer than 190 different species of plants (belonging to 89 genera) being given as hosts, observes: "Freilich, ob diese Anschauung berechtigt ist, ist bis heute durch nichts bewiesen. Es liegen nämlich nur ganz vereinzelte auf culturversuche begründete Bestätigungen dieser gewöhnlich in extenso angenommenen Voraussetzung vor, was um so mehr auffallen muss, als doch bei anderen Pilzfamilien, z. B. den Uredineen, trotz der dort bestehenden grösseren Schwierigkeiten, die Frage der Wirthzugehörigkeit für eine grosse Anzahl von Arten durch experimentelle Untersuchungen klargelegt worden ist." Further, with reference to the fact that in my monograph a great reduction of species was made, Neger remarks : "Inwieweit dieses summarische Verfahren berechtigt ist, muss die Zukunft lehren. Hieraus ergibt sich aber das zweite, einer Lösung dringend bedürftige Problem : Welcher der bisher auf gestellten, auf morphologische Merkmale begründeten Erysipheenarten erweisen sich physiologisch als solche? oder um die von Rostrup bei den Uredineen angewandte Bezeichnung zu gebrauchen : Werden nicht viele der bisher als morphologisch gleich erkannten Formen in 'biologische' Arten aufzulösen sein?"

The question of the possibility of the occurrence of "biological species" in the Erysiphaceae is one of primary importance, not only from the scientific side, but also from the economic point of view—for if "biological species" do exist, then we should endeavor to ascertain if the species of mildew which cause such widespread damage to cultivated plants belong to this class. If, for instance, it were found that the "hop-mildew" constituted a "biological species," then we should know from which of the common weeds of the hop garden (*Spiraea, Ulmaria, Potentilla* spp., *Epilobium* spp., etc.) which serve as the host-plants of the morphological species called *Sphaerotheca humuli*, it could pass on to the hop; or whether, as might possibly prove to be the case, the spread of this hop-disease is dependent on infection from hop-plant to hop-plant.

It will be well here to review the evidence with regard to this point. Direct experiments, and observations bearing on the subject are, so far as I am aware, very few in number. The experiment of taking the conidia of a mildew growing on a certain host-plant, and sowing them on the leaves of another plant has been performed by three botanists : (1) Magnus (in Bericht. deutsch. bot. Gesellsch. **16** : 68. 1898) has stated that the conidia of *Sphaerotheca humuli* (DC.) growing on the hop will germinate and produce a conidia-bearing mycelium when sown on the leaves of *Taraxacum officinale*. (2) Iwanowsky (**32**) made some experiments in connection with the *Oidium** occurring on the tobacco plant. Iwanowsky observed an *Oidium*, which he referred to the conidial form of "*E. lamprocarpa*" (= *E. cichoraccarum*), occurring on the leaves of some Compositae, especially *Inula Helenium* and *Lappa tomentosa*. This *Oidium* he found on examination to resemble strongly the *Oidium* on the tobacco plant. To quote the author's words: "Bei der Aussaat dieser Conidien auf die Blätter der Tabakspflanze entwickelte sich in der That das Tabaks-*Oidium;* hieraus folgt, dass Letzteres zu *Erys. lamprocarpa* gehört; jedoch bildet dieser Pilz auf dem Tabak keine Fruchtkörper. In Form von Fruchtkörpern überwintert er auf den genannten Compositen und inficirt im folgenden Sommer die Tabakspflanze." (3) Neger (**54**, p. 339) records the following observations: "Auch das Nährsubstrat scheint Einfluss zu haben auf die äussere Gestalt der Conidien. Ich übertrug Conidien von *Erysiphe communis*, welche auf *Ranunculus* sp. entstanden waren, auf eine vollkommen gesunde, unter einer Glasglocke stehende Pflanze von *Galium silvaticum;* die Infection gelang; nach einigen Tagen trug das *Galium* Rasen von Conidien-trägern. Der Vergleich ergab, dass die Conidien auf *Galium* beträchtlich länger waren als diejenigen auf *Ranunculus*."

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* This *Oidium* De Thümen described as *O. tabaci*; it is in all probability the conidial condition of *Ery iphe cichoracearum* DC. (see monograph, p. 294).

Cases apparently showing that in nature a species of mildew on one host-plant sometimes passes over to a contiguous plant of another species are mentioned by two botanists: (4) Allescher (in the Bericht. botan. Verein. Landshut, 146–152. 1887) has recorded the occurrence of *Microsphaera Ehrenbergii* (= *M. alni* var. *lonicerae*) on *Syringa vulgaris*, and has stated that the *Syringa* affected stood in the immediate neighborhood of a bush of *Lonicera Tatarica* attacked by the same fungus. On Allescher's specimen sent to me it was noted that the fungus occurred only on the branches of the *Syringa* which were close to the *Lonicera*. (5) Brannon (**8**) has recorded "*Erysiphe communis* (Wall.) Schl." occurring "on *Ranunculus recurvatus* and an aster growing in the same place which had probably received the mildew from its neighbors."

(6) Polla (in Bericht. deutsch. bot. Gesell. **17**: 67. 1899) has made some observations bearing on the present subject. This author, having observed that in certain districts only *Berberis vulgaris* and *Corylus Avellana* were attacked by *Phyllactinia*,

while other trees, growing intermixed with the *Berberis* and *Corylus* (such as *Carpinus, Betula, Fagus, Fraxinus,* etc.), which in other districts are liable to be attacked, here remained perfectly free from the *Phyllactinia,* was led to the conclusion "dass *Phyllactinia suffulta* eine Sammelspecies darstellt, and dass die auf den verschiedenen Nährpflanzen beobachteten Formen, wenn auch vielleicht nicht eine jede einer besonderen, doch mindestens mehreren verschiedenen, morphologische einander sehr ähnlichen oder gleichen Arten angehören, welche nur auf ganz bestimmten Nährpflanzen gedeihen. Zweifelsohne liegt bei *Phyllactinia* und wohl auch noch anderen Gattungen der Mehlthaupilze bezüglich der Speciesfrage dieselbe Erscheinung vor, wie sie bei den Rostpilzen aufgedeckt worden ist und als *Specializrung des Parasitmus* bezeichnet wird."

Reviewing the experiments given above, I should like to point out with reference to those, (1), (2) and (3), in which conidia were taken from one host-plant and sown on another, that such experiments require the greatest precautions being taken to ensure that the plant on which the conidia are sown has not been naturally infected previous to the experiment, and that it is not liable to infection during the course of the experiment. Two cases which show the necessity of the greatest care being taken in this direction have come under my notice. A plant of *Cineraria,* taken direct from a greenhouse in which the plants were apparently free from mildew, was placed in a greenhouse where the cinerarias were badly affected with *Oidium,* and kept covered over by a bell-jar. Experiments were made with the object of trying to infect this *Cineraria* with an *Oidium* occurring in the same greenhouse on *Celsia,* and for this purpose the bell-jar was removed two or three times to allow the placing of the *Oidium*-conidia on the leaf, and subsequently to observe if infection had taken place. The experiment failed, as on the marked places on the *Cineraria*-leaf where the conidia of the *Celsia-Oidium* were sown, no *Oidium* appeared. In other spots on one or two of the leaves experimented with, however, an *Oidium* began to grow, and spread gradually in large patches over the leaf, producing conidiophores in large numbers. A microscopic examination of the conidia of this *Oidium* showed that it resembled the *Oidium* that grew on the cinerarias in the greenhouse, the conidia differing from those of the *Oidium* on *Celsia* in being smaller and in possessing distinct fibrosin-bodies. It is clear, therefore, that infection must have taken place by some means from the adjacent cinerarias.

In the second case, some rose bushes in a garden were observed covered with an *Oidium*, and it was noticed after a few days that an *Oidium* had now appeared on some adjacent raspberry suckers. To ascertain if the rose-*Oidium* had really, as it appeared, spread from the rose to the raspberry, the following experiment was carried out. The raspberry suckers, mentioned above, which were attacked by the *Oidium*, were situated on one side of a garden path; on the other side of the path were two isolated suckers, both of which at this time showed no signs of *Oidium*. On one of these, conidia taken from the rose were sown, and the sucker covered over with a bell-jar. The next day it was found that this sucker was slightly attacked by an *Oidium*, which in the course of a few days spread and showed itself on most of the leaves at the apex of the sucker. During the whole time, the adjacent sucker, left untouched and uncovered, remained free from any *Oidium*. It might readily have been assumed that we had here the proof of the passing of an *Oidium* from one species of host-plant to another, but a microscopic examination showed that such was not the case. The shape of the conidia on the raspberry plants agreed exactly with that of the conidia of *Sphaerotheca humuli* (this species is recorded on the raspberry by Burrill in Ellis and Everh., N. Amer. Pyrenomycetes), and differed from that of the conidia on the rose (*S. pannosa*) in shape and size. The difference between the conidia of *S. humuli* and *S. pannosa* I have elsewhere pointed out (71). On examining the *Oidium* which appeared on the raspberry sucker experimented upon, the conidia were found to agree in shape with those of *S. humuli* and not of *S. pannosa*. It might be suggested, of course, that the difference in shape was due to the influence of a different species of host-plant on the same species of fungus, but in the face of repeated experiments (made in a garden where no raspberry-*Oidium* occurred) in which it was found that conidia taken from the rose and sown on raspberry suckers invariably failed to produce any infection, we are forced to conclude that in the first experiment mentioned above the raspberry sucker must have been already naturally infected by the *Oidium* on the raspberries before being experimented upon.

With regard to Magnus' experiment (1), I have already (monograph, p. 18) pointed out the special difficulties which arise if we consider that the *Oidium* which appeared on the *Taraxacum* really resulted from the sowing of the conidia of *S. humuli* from the hop.

Experiment (2) would seem, if scientific precautions were taken to prevent the access of other conidia to the tobacco leaf under observation, to prove satisfactorily that *Erysiphe cichoracearum* can pass from the leaves of a host-plant belonging to the Compositae to one belonging to the Solanaceae.

The acceptance of the conclusions drawn by Neger from his experiment (3) involves us in the same difficulties as in the case of Magnus' experiment. If the conidia of *E. polygoni* were really the ones that produced the *Oidium* on the *Galium* (the fact that the *Galium* plant was kept under a bell-jar does not, unless special precautions were taken, preclude the possibility of infection by other conidia having taken place) it seems strange that we do not find in nature *E. polygoni* occurring on *Galium*. It is true that many authors have recorded "*E. communis*" or "*E. Martii*"—synonyms of *E. polygoni*—on species of *Galium*, chiefly *G. Aparine*, but this has always been due, I believe, to a wrong identification of the fungus having been made, as in all cases investigated the fungus has proved to be *E. cichoracearum* (see monograph, p. 20). It is to be noted, too, that Neger expressly states that the *Oidium* which appeared on the *Galium* showed morphological differences from that on the *Ranunculus*—a fact certainly favorable to the idea that infection from some other source had taken place.

With regard to case (4) I have, through the kindness of Professor P. Magnus, seen Allescher's specimen of "*M. Ehrenbergii*" on *Syringa vulgaris*. The fungus, which is certainly growing on this host, as the presence of mycelium and young perithecia show, presents the characters of the var. *lonicerae* (=*M. Ehrenbergii*) rather than those of the *M. alni* type (which grows commonly on *Syringa vulgaris* in the United States). It seems, therefore, that we can, as Magnus (Bericht. deutsch. bot. Gesellsch. **16** : 68. 1898) has done, accept the case as affording proof that the var.

lonicerae has here passed over from the *Lonicera Tatarica* to the *Syringa.*

(5) I have not seen a specimen of the *Erysiphe* on *Aster* referred by Brannon to "*E. communis.*" If the fungus has been correctly determined, it would be a remarkable instance of the passing over of the species to an unusual host-plant, as the *Erysiphe* which occurs so commonly on *Aster* in the United States has hitherto invariably proved to be *E. cichoracearum.*

It has long been noticed (*cf.* Léveillé, Ann. Sci. Nat. III. **15**: 219. 1851), that certain species of the Erysiphaceae, or examples of a species on a certain host-plant, only rarely, or (in the second case) perhaps never, produce perithecia. In connection with this subject Neger (**54**) asks the question: "Von welchen Factoren hängt die Conidienbildung, von welchen die Perithecienbildung ab?" With a view to obtain evidence on the subject, Neger kept under observation species of mildew growing on *Artemisia vulgaris*, *Ranunculus*, and *Epilobium montanum.* These were first kept at a room-temperature in a damp atmosphere under bell-jars, and it was found that under these conditions the formation of conidia was extremely luxuriant, but that no formation of perithecia took place. Afterwards, in November, the plants were placed in a cold greenhouse, in which the temperature and atmospheric conditions were similar to those occurring in the open at the normal time for the production of perithecia. It was then found that no perithecia were formed on these plants. Neger remarks also, that in nature no production of perithecia takes place, as a rule, on those host-plants which have been injured by an excessively heavy crop of conidia, and cites *Uncinula necator* on *Vitis*, *Sphaerotheca pannosa* on roses, and *S. Castagnei* on *Spiraea* as examples. Also, it is observed that when the development of conidia is slight, then an abundant formation of perithecia occurs, *e. g.*, *Microsphaera alni* on *Viburnum Lantana*, *Phyllactinia corylea* and *S. Castagnei* on *Comarum palustre.* Neger, as a deduction from these facts, and from the results of his single series of experiments, believes that an answer to the question stated above can be given as follows: "Conidienbildung wird befördert durch einen aus frischen, turgescenten Pflanzentheilen bestehenden Nährboden. Temperatur- und Feuchtigkeitsverhältnisse scheinen von untergeordneter Bedeu-

tung zu sein. Perithecienbildung setzt einen aus älteren (meist ausgewachsenen) Pflanzentheilen bestehenden und durch Conidienfructification noch nicht erschöpften Nährboden, sowie ein mehr oder weniger reich entwickeltes Luftmycel voraus."

I cannot agree with Neger that he has here given the causes which account for the formation or non-formation of perithecia in the Erysiphaceae. We find in nature so very frequently perithecia produced on the same leaf by the mycelium which had previously produced conidia that I am inclined to look upon this as the normal course of development, and to consider the non-production of perithecia on conidia-bearing mycelium as exceptional, instead of *vice versa*, as we should be obliged to do if we accepted Neger's view. In many cases, the non-production of perithecia seems undoubtedly connected with the influence of certain host-plants on the fungus ; *e. g.*, it is only in rare cases (see monograph, p. 202) that *Erysiphe cichoracearum* produces perithecia on cultivated plants of *Cucumis* and *Cucurbita.* Further, it is to be noted that when perithecia do occur, they are found (in the case of the fungus on *Cucurbita Pepo* (vegetable marrow), not on distinct parts of the host-plant, but in the midst of the parts covered with the *Oidium*-bearing mycelium. Exactly the same occurs in the examples of *E. cichoracearum* on the tobacco plant. On several species of *Myosotis* an *Oidium* occurs which has been commonly referred to *E. cichoracearum*, but neither on living plants, nor on the numerous specimens in exsiccati and herbaria, have I ever been able to find any perithecia. In conformity with the rule which obtains for many parasitic fungi, the normal course of development for the Erysiphaceae consists of two phases—a conidial stage in which successive crops of conidia are produced during the summer months when the host-plant is growing vigorously, followed (omitting exceptional cases) by a formation of perithecia at the time when the life of the host-plant begins to fail, so that resting-spores (here represented by the ascospores are formed in order to continue the life of the fungus in a dormant condition through the winter when no host-plants are available. This relation to food-supply may be compared with the well-known fact of the production in the Zygomycetes of zygospores, which can be artificially induced at any time by diminishing the food supply of the fungus.

It may be remarked here that little is known in connection with the germination of the ascospores. Wolff succeeded in germinating those of *Erysiphe graminis*, and in infecting grass leaves with them, but apparently no one since has repeated the experiment. Galloway germinated the ascospores of *Uncinula necator*, but failed in all attempts to infect leaves with them. In September, 1900, I placed a number of leaves bearing ripe perithecia of *Erysiphe tortilis* on the ground. These leaves were fully exposed to the weather, and were kept in every way under natural conditions. From time to time during the winter the dried remains of the leaves bearing still numerous perithecia were examined, but no opening of the perithecium or change in the appearance of the asci or ascospores was found. Finally, in the early summer of the next year, all the material was examined, consisting of about twenty perithecia on fragments of leaves, and it was then found that externally the perithecia appeared quite unchanged. On opening the perithecia it was found that many of the ascospores had collapsed, and in the surviving ones no germination could be induced. It may be worth noting that in *E. tortilis* the appendages of the perithecium are very persistent, being found little changed at the end of eight or nine months of exposure. In *U. necator* Galloway found that the appendages soon disappeared on exposing the perithecia to the weather.

With regard to the sudden appearance of "*Oidium*" on plants, it has long been remarked that it is especially liable to occur after cold nights. Some experiments I have made (71) in connection with the germination of conidia seem to give some direct evidence on this subject. In the case of *S. humuli* on strawberries it was found that the conidia when sown in hanging drops at ordinary temperature showed only a feeble germination. On subjecting the conidia, however, before being sown to a low temperature—either by placing them on blocks of ice, or by subjecting leaves bearing conidia to a temperature of 0° C. the germinating power shown subsequently was very perceptibly greater. As I have already (71) remarked, it would appear, therefore, that in nature a decrease of temperature may cause plants to be attacked by mildew, not only because the vitality of the plants may perhaps be weakened, and so rendered less able to withstand the attacks of parasites, but also by directly increasing the germinating powers of the spores of the parasitic fungus. Eriksson (" Ueber die Förderung der Pilzsporenkeimung durch Kälte," Centralbl. für Bakter. und Parasitenk. **1**: 557–565. 1887) has also experimented on the same lines with regard to the germination of uredospores, and found that cooling down to freezing point had a favorable influence on their germinating powers.

As Zopf (**90**) has pointed out, bodies of a definite shape are found in the cell-contents of the conidia of certain species of the Erysiphaceae. These bodies are composed of a substance which Zopf calls fibrosin, and which he states to be almost indistinguishable in its reactions from fungus cellulose. The bodies are minute, the largest measuring 6–8 μ in the greatest diameter, and are of varied shape, flattened discs, conical and hollow, or cylindrical. These fibrosin bodies belong to the group of carbohydrates, and according to Zopf function as reserve material; he observed that on the germination of the conidia the fibrosin bodies were gradually absorbed. They were first observed in the conidia of *Podosphaera oxyacanthae*, but were also seen by Zopf in *Sphaerotheca* and in some species of *Erysiphe*. Neger (**54**) has observed them well-developed in the conidia of species of *Uncinula*, but states that in *Microsphaera* they appear to be absent or almost too small to be visible. Zopf's statement, however, that these fibrosin bodies constitute the only case known in fungi in which a carbohydrate serves as reserve material—in the place of fat or oil—is erroneous, as other carbohydrates are known to occur not uncommonly (see Errere in Ber. deutsch. bot. Gesellsch. **5**: lxxvi. 1887).

Harper in an important paper in the Annals of Botany (**25**), in which the question of relationship of the Erysiphaceae to other fungi is discussed, replies in detail to the article of Dangeard (**14**) in which an attempt is made to discredit Harper's previously published account of the development of the perithecium in *Sphaerotheca*.

I am indebted to the following botanists for kindly sending me specimens: Professor J. C. Arthur, Mme. J. E. Bommer, Professor F. Bubák, Professor A. Mágócsy-Dietz, Mr. E. M. Freeman, Dr. J. Feltgen, Dr. D. Griffiths, Dr. P. Hennings, Professor Shotaro-Hori, Professor A. Jaczewski, Professor A. Kitmanoff, Dr. E.

Lambotte, Dr. G. Lnstner, Professor P. Magnus, Professor Kingo Miyabe, Dr. F. W. Neger, Dr. N. Patouillard, Professor E. Rostrup, Professor P. A. Saccardo, Dr. C. Spegazzini, Dr. R. Tolf.

(To be continued.)